

Article XXXIII.—ON THE STRUCTURE AND AFFINITIES OF
BOLOSaurus.

By ROBERT BROOM.

In 1878 Cope described under the name *Bolosaurus striatus* the skull of a small reptile from the Lower Permian of Texas. The type skull (Am. Mus. 4320) is very unsatisfactory though the structure of the molar teeth can be clearly made out. One other skull in the Cope Collection (Am. Mus. 4327) shows considerably more of the cranial structure, but apparently Cope has not very carefully examined it. A third skull (Am. Mus. 4461) I regard as belonging to a distinct species.

In 1906 Case discovered at Godlin's Creek, Texas, two small skulls and the crushed jaws of another and a large number of associated vertebrae with portions of shoulder girdle and limbs of an animal which he believed to belong to Cope's species. These he described in 1907, and repeated the description with figures of both skulls in his "Revision of the Cotylosauria of North America" in 1911. He places *Bolosaurus* as Cope had done in a distinct family the Bolosauridae and puts it with the family Diadectidae—the two families forming the Suborder Diadectosauria of the Order Cotylosauria.

In 1911, v. Huene while in America appears to have seen the principal *Bolosaurus* material, but he gives no new figures and makes only one new observation. He says, "the teeth refer *Bolosaurus* to the Diadectidae and with equal certainty the skull base indicates the same group. . . . In the original I can see nothing of the great post-temporal opening which Case assumes in his paper on *Bolosaurus*."

As I had long felt very strong doubts about *Bolosaurus* being a Diadectid at all I was very anxious to have an opportunity to examine the fine series of specimens in the American Museum, and through the kindness of Dr. W. D. Matthew I have been enabled to carefully examine all the specimens. One sometimes wonders whether science is advanced more by a new worker agreeing with those who have previously studied the same fossils or problems, or by his differing from them. Agreement may long fix an error, but a difference of opinion is pretty certain to lead to further investigation and the ultimate truth. It would thus appear that an honest difference is less harmful than too ready acquiescence. In regard to the specimens grouped together as *Bolosaurus striatus* I regret that my opinions differ very considerably from those of Cope, Case, and v. Huene. So far from regarding all the specimens as belonging to one species I believe they belong to three different species and two different genera, and I further

differ from Cope, Case, and v. Huene in believing that none of the three species is in any way nearly related to *Diadectes* and that all belong to quite a different order.

Before dealing with the question of affinities it may be well to make a systematic revision of the group.

***Bolosaurus striatus* Cope.**

To the type species I refer the large majority of the remains. Besides the type skull No. 4320, the following skull remains belong to the type species:—4321 a crushed skull in very bad condition but showing the teeth fairly satisfactorily; 4462 crushed jaws showing the teeth satisfactorily; 4322 fragment of left mandible figured by Case, showing the posterior molars to perfection; 4324 badly crushed snout and jaws showing the teeth fairly; 4326 crushed jaws with fair teeth; 4327 a fairly good skull considerably crushed but practically complete with a number of teeth in fair condition; also many other imperfect jaw fragments, vertebræ and fairly well preserved pelvis.

***Bolosaurus major* sp. nov.**

This new species I found on the imperfect skull, No. 4461. It agrees sufficiently closely with *B. striatus* to leave little doubt that it belongs to this genus, but it differs from *B. striatus* in being larger and in having much larger teeth. From the large series of jaws of *B. striatus* which are practically identical in tooth measurements we may safely assume that the specimens are fully grown and that this much larger form belongs to a distinct species.

The skull is badly preserved, but shows in satisfactory condition the left maxilla, left prefrontal, both frontals, the left parietal, and postfrontal, and in a less satisfactory condition a number of other elements. The teeth differ from those of *B. striatus* in being larger and in having relatively higher crowns. In *B. striatus* the four largest maxillary teeth measure together 7.5 to 8 mm.: in *B. major* the four largest teeth measure 10 mm.

***Ophiodeirus casei* gen. et sp. nov.**

This new genus and species is founded on the small forms discovered by Case in 1906, and believed by him and v. Huene to belong to *Bolosaurus striatus*. There is not I think the slightest doubt that the skulls 4685 and

4686 belong to the same species but to avoid any possibility of confusion 4685 will be regarded as the type, as it shows the palate very satisfactorily and the teeth better than skull 4686.

The differences between *Ophiodeirus casei* and *Bolosaurus striatus* are considerable. Besides the marked difference in size the teeth are very different. In *B. striatus* there are eleven teeth in the upper jaw and ten in the lower. From the third there is a steady increase in size to the second last — the last two being of about equal size. In *Ophiodeirus casei* there are sixteen teeth above, and probably about as many below, and they are much more uniform in size. The 11th, 12th and 13th teeth are a little larger than the others and behind the 13th they steadily decrease in size. The structure of the teeth also differs markedly from those of *B. striatus*. In it the posterior teeth of the upper jaw have a large main cusp with behind and slightly internal to it a second small cusp. The axis of the two cusps is from 30° to 45° to the right or left of the middle plane. In the lower jaw the main cusp is behind and the second small cusp lies about 10° to the outside. Case in 1907 gave excellent figures of the posterior teeth of the left lower jaw of *Bolosaurus striatus* though in error the figure is marked "upper jaw." In *Ophiodeirus casei* the anterior teeth are round, and the posterior ones are flattened, giving the crown a narrow transverse surface with two low subequal cusps and a shallow valley between them. In none of the teeth is the crown fully displayed, but enough is seen to show that it is quite different from that of *Bolosaurus striatus*.

A more difficult question arises as to how far *Ophiodeirus* is distinguishable from *Aræoscelis* of Williston described in 1910. Without question the vertebræ figured by Williston are those of a form nearly allied to *Ophiodeirus*. The humerus however is much larger than the humerus of *Ophiodeirus*.

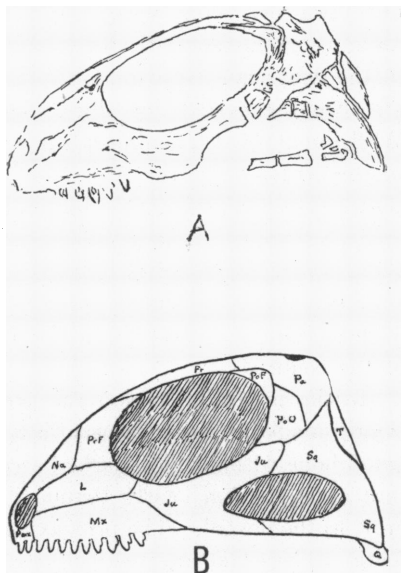


Fig. 1. A. Skull of *Bolosaurus striatus*. Slightly enlarged.

B. Skull of *Bolosaurus striatus*. Attempted restoration. The only part of the restoration that is in much doubt is the lower arch. There is no evidence as to whether it is formed of jugal, squamosal or quadratojugal. There is evidence for most of the rest of the restoration.

deirus and if his restoration of the skull is nearly correct there is no doubt the forms are generically distinct. In any case they are certainly specifically distinct.

Structure and Affinities of the Bolosauridæ.

Seeing that Prof. Williston has got some good skeletons of *Aræoscelis* only awaiting being worked up it might seem inadvisable to discuss the affinities of the family from the poor remains of *Bolosaurus* and *Ophiodeirus* in the American Museum. But as *Bolosaurus* and *Ophiodeirus* have hitherto been believed to be allied to *Diadectes*, and *Aræoscelis* is believed by Williston to be a Theromorph it will be necessary to look into the details of the structure of the American Museum Bolosaurids in order to prove that *Aræoscelis* belongs to the same family.

Unfortunately none of the Bolosaurid skulls in the American Museum shows the structure of the temporal region satisfactorily, though specimen 4327 reveals a considerable number of facts. In figure 1 A I give a side view of the specimen as preserved and in figure 1 B an attempt at an interpretation of the elements.

In the preorbital region the prefrontal, maxilla and premaxilla can be clearly made out and the nasal less satisfactorily. The maxilla is an elongated bone without any marked ascending process which makes it probable that as in so many early Permian reptiles the lacrymal extends from the orbit to the nostril. The premaxilla is small, and appears to have only two teeth. These like the teeth of the maxilla and mandible are ankylosed to the bone — another marked point of difference from the teeth in *Diadectes* where they are thecodont. The prefrontal forms the upper anterior side of the orbit as in *Sphenodon*. The frontals are well preserved in a number of *Bolosaurus* specimens. They are fairly broad and form the upper orbital margins.

The parietals are about as large as the frontals. Between them and nearer the back than the front of the bone is a large pineal foramen. Along the upper and posterior border of the orbit is a fairly large but narrow curved postfrontal. Below it and between it and the jugal is the postorbital. It meets above the parietal and posteriorly and inferiorly the squamosal. The jugal is a large bone which forms much of the orbital margin and meets both the squamosal and postorbital above. It is not clear whether the zygomatic arch is formed by the jugal or by the squamosal or by the quadratojugal—probably mainly by squamosal. The squamosal is a large bone which forms most of the suspensorium as in *Sphenodon*. It meets the parietal above and the postorbital and jugal in front and extends down nearly to the articu-

lation. The occiput is closed in at the sides there being so far as I can make out no openings such as figured by Case. In fact where Case figures the



Fig. 2. Cervical and dorsal vertebrae of *Ophiodeirus casei*. About $\frac{2}{3}$ natural size. The last four vertebrae, probably c6, c7, d1, and d2, are found attached in the specimen. The others, probably c3, c4 and c5, are detached vertebrae.

opening there is a very large flat bone presumably the tabulare. The occipital condyle is small and rounded and very unlike the condyle of *Diadectes*.

The mandible is almost Therapsid in structure. There is a large dentary, and a fairly large angular. The surangular lies above the angular as in the *Anomodonts*. The splenial is very well developed and extends well back inside the angular.

Many of the vertebrae of *Ophiodeirus casei* are well preserved. All have slender centra with for the most part broad arches. The centra are notochordal and there is a small intracentrum between each pair. The anterior dorsal vertebrae have well developed transverse processes near the anterior end of the vertebra from which a ridge descends to the anterior edge of the articular surface of the centrum. At the lower part of this ridge is a thickening for the head of the rib. The spines are short and by their sides are small mammillary processes presumably for the support of small dermal ossicles. The posterior dorsals have the arches considerably broader and have them lightened by a deep excavation on the side as also figured by Williston in *Aræoscelis*.

The cervical vertebrae are very remarkable in being greatly elongated and slender. By both Case and Williston they have been mistaken for caudals. But there is not the slightest doubt about their being cervicals. In Case's specimens of *Ophiodeirus casei* there are two series of dorsals and cervicals

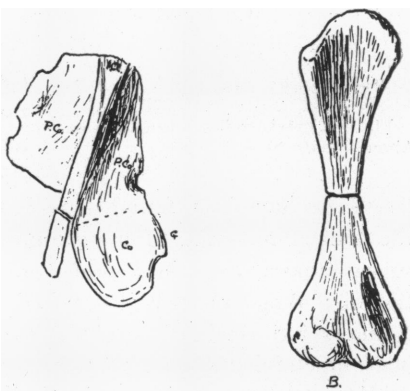


Fig. 3. A. Coracoid, both precoracoids and interclavicle of *Ophiodeirus casei*. About $\frac{2}{3}$ natural size.

B. Right humerus of *Ophiodeirus casei*. About $\frac{2}{3}$ natural size.

with the vertebræ in contact, the smaller of which I figure with three other cervicals which are probably 3rd, 4th, and 5th. There has not been found in the collection any vertebræ that is manifestly the axis but I assume four elongated cervicals is about as many as *Ophiodeirus* is likely to have had. The cervicals have very short rudimentary spines only the supposed 6th and 7th having mammillary processes. The cervical vertebra of *Aræoscelis* figured by Williston is probably the 3rd cervical. It is relatively more slender than the corresponding vertebra of *Ophiodeirus* but otherwise very similar. The few caudals preserved in the collection are all smaller than the dorsals and all short. The sacrum is I think correctly stated by Case to be formed of two vertebræ. The 1st and 2nd caudals have long curved riblike processes like those of *Procolophon*.

Of the shoulder girdle the only remains are the left coracoid and part of the precoracoid, most of the right precoracoid and much of the interclavicle.

The right humerus is in nearly perfect condition. The contact between the upper and lower parts is missing, but probably extremely little of the bone is lost. Assuming nothing is missing the bone measures 38.5 mm.

The pelvis is preserved in fair condition. Much of both pubes and ischia are present, and though considerably crushed both bones can be restored with confidence. The right ilium is practically complete but also crushed. In the figure I have given a restoration of the pelvic elements.

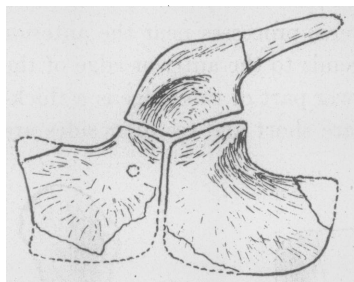


Fig. 4. Pelvis of *Bolosaurus striatus*.
About $\frac{2}{3}$ natural size.

In discussing the affinities of the *Bolosauridæ* one is again hampered to a considerable extent by our present ignorance of the structure of some possibly allied forms. Though large numbers of specimens of *Palæohatteria* and *Pro-*

torosaurus have been found there is room for much further study even on the known material. For example we do not know whether there is a supratemporal fossa in *Palæohatteria*. Credner and others have believed there is; Watson and Williston believe there is not. Then almost nothing is known for certain of the skull of *Protorosaurus*, and one feels one cannot place much reliance on Seeley's restoration.

When the restoration of the skull of *Bolosaurus* was made, without any thought for the time of what might be its affinities, the striking resemblance to that of *Palæohatteria* was at once manifest. Doubtless there are many differences and important differences, but if Watson is right that there is

no supratemporal fossa than one is forced to admit the probability of some affinity between the forms. The degree of affinity however cannot be very close. *Palæohatteria* like *Varanosaurus* has lost the true coracoid, which *Ophiodeirus* retains and it must thus be distinctly more primitive than either of the former genera.

With *Protorosaurus* in the absence of any very satisfactory knowledge of the head a comparison is difficult. The fact that *Protorosaurus* has the similar unusual characters for early reptiles of elongated cervical vertebræ suggests a possible relationship, but probably this resemblance does not indicate any near affinity. The fact of *Bolosaurus* and *Ophiodeirus* having well developed sclerotic plates, and probably both, certainly the former, having abundant abdominal ribs strengthens the resemblance to *Protorosaurus* and also to *Palæohatteria*.

With *Varanosaurus* and the allied *Pæcilospondylus* and *Poliosaurus* the affinities are much clearer. In the structure of the pelvis there is a very

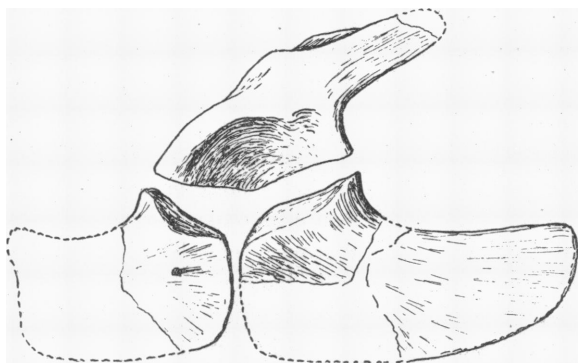


Fig. 5. Pelvis of *Pæcilospondylus francisi* Case. About $\frac{3}{4}$ natural size.

distinct resemblance to that of the first two of those genera. All have the broad plate-like pubes and ischia and the narrow backwardly directed ilium. The shoulder girdle of *Varanosaurus* differs in having lost the true coracoid. The shoulder girdle is unknown in the others. The humerus agrees closely with that of *Varanosaurus* and *Pæcilospondylus* but this in itself is not a character of much importance. The detailed structure of the skull of *Varanosaurus* is not yet known, but in essential structure except in having lost the jugal arch it is probably not remarkably different from that of *Bolosaurus*.

With the Pelycosaurs proper there are some other evidences of affinity, such as a close agreement in the structure of the lower jaw and the shoulder girdle and considerable agreement in the structure of the vertebræ.

When the skull of *Aræosceles* is fully known it will probably be seen that there is considerable agreement between it and the South African Droma-

saurians. The shoulder girdle of *Bolosaurus* is liker that of *Galepus* than it is to any of the other known American types. The large size of the squamosal with its descent to near the articulation of the jaw is another feature suggesting some affinity.

It might be thought that this large number of different groups with which there seem to be affinities is too great to be probable, and that some of the supposed affinities may be accounted for by convergence. Convergence may explain certain resemblances, but convergence is being appealed to nowadays to far too great an extent, and resemblances are only due to convergence in probably a small minority of cases.

In the present state of our knowledge it seems probable that the Bolosauridæ represent a group of primitive "Theromorphs" near to the common ancestors of the Pelycosaur, Varanosaurids, and Dromasaurians. Even without knowing anything of the Bolosauridæ we know that these three groups had a common post-Cotylosaurian ancestor and while the Bolosaurids are too specialised to have been ancestral they are probably members of the suborder that included the common ancestor. If we place the Bolosauridae in this central position we get a satisfactory explanation of its seeming varied affinities. And when we find Williston maintaining that *Palæohatteria* is extremely closely allied to *Varanosaurus* we can understand the apparent resemblances between it and the Bolosaurs. Williston in fact expresses himself as unaware of any important character separating *Palæohatteria* from the American types such as *Varanosaurus* except the absence in the latter of sclerotic plates. The discovery of sclerotic plates in *Bolosaurus* and *Ophiodeirus* removes even this barrier. Sclerotic plates are known in the African Dromasauria and the Anomodontia and were probably present in the early types of the mammal-like reptiles.

Watson discovered in South Africa in beds of the *Pareiasaurus* zone a small reptile which he believes to be very closely allied to *Aræoscelis*. The top of the skull is unknown though the palate is beautifully preserved and most of the postcranial skeleton. Until Watson's description is published I shall refrain from discussing its possible affinities to the Bolosauridæ.

Another South African form that may be referred to is *Procolophon*. Though it is convenient as a matter of classification to keep this little lizard-like form in the Cotylosauria on account of its having a roofed temporal region it differs very greatly from Cotylosaurus such as *Diadectes* and also very considerably even from *Pareiasaurus* or *Captorhinus*. A good many years ago I pointed out that *Procolophon* in many ways resembled *Palæohatteria*. The Bolosauridæ show very suggestive resemblances to both. In the skull they are nearer to *Palæohatteria*, *Varanosaurus* and the Dromasaurians, but in the shoulder girdle the resemblance to *Procolophon* is very marked.